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STRAITS SETTLEMENTS

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CONTENTS.

THE IDENTIFICATION OF THE BROWN-ROOT FUNGUS.

Page

By E. J. H. Corner, M.A. 317

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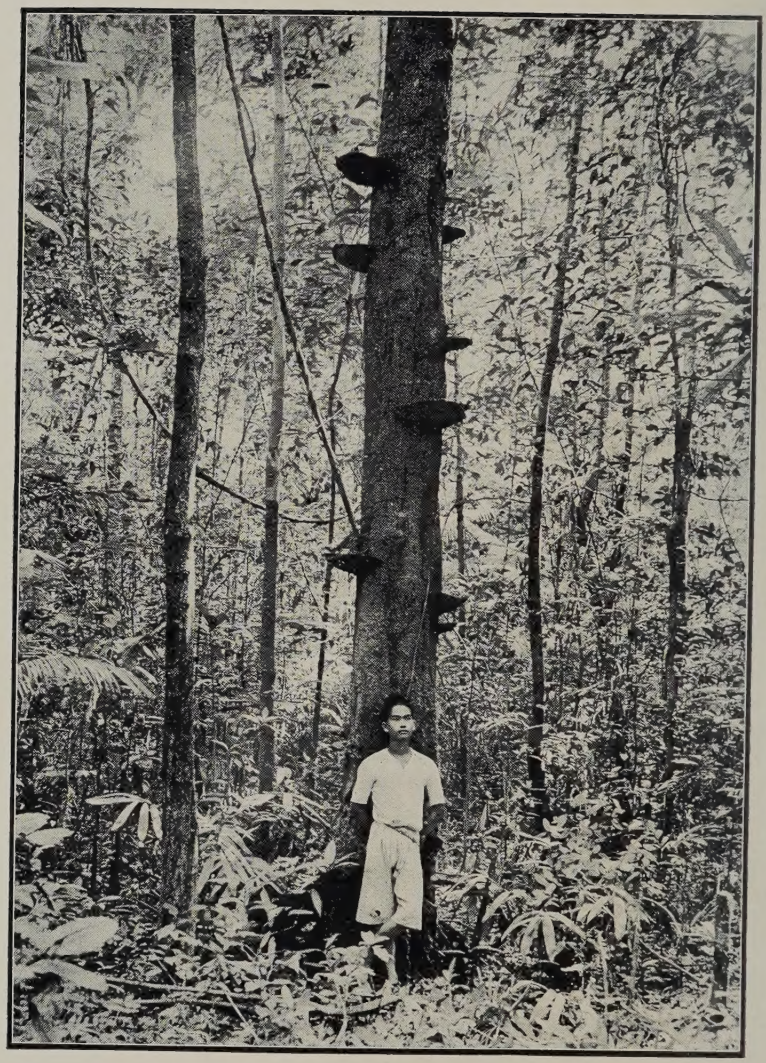
Volume V no. 12 completes Vol. V of the Gardens' Bulletin; with it is despatched a title page and index.

Volume VI, consisting of three parts and dealing with native medicine in the Malay Peninsula, was issued concurrently with Vol. V, and is already completed.

Subscriptions to Volume VII are now due. The subscription to this volume will be $8.00 in the Malay Peninsula and £1 outside, post free. It will consist of about 380 pages, and will be issued in parts at irregular intervals. The separate prices of the parts will be fixed according to their size.



Some large fruit-bodies of *Fomes lamaensis* growing on a dead standing trunk in swamp-forest, Sedili River, Johore, 1931.

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THE IDENTIFICATION OF THE BROWN-ROOT FUNGUS

By E. J. H. Corner, M.A.

Two species have been called *Fomes lamaensis* (Murr.) Sacc. et Trott. The one which rightly bears the name is a harmless saprophyte; the other, which I propose to call *F. noxius*, is a facultative parasite and it is the cause of the Brown-root disease of rubber-trees and tea-bushes and, as it seems, of the stem-rot of oil-palms which Thompson has recently described (9). The confusion arose through an error of Lloyd's in referring to *F. lamaensis* specimens of the Brown-root fungus which Petch had sent from Ceylon, and his identification is now current in the phyto-pathological literature (8). The two species are extremely close; in mycelial characters and in the general construction of the fruit-body they are indistinguishable; and there is evidence that they may hybridise. But they differ in certain microscopic details of the fruit-body and once these are understood they cannot be mistaken. Only after the minutest investigation, however, has it been possible to state these distinctions clearly. The results show too well how misleading may be the attempts to recognise polypores from their macroscopic characters, not merely because in the tropics there are so many radically different species which are superficially alike, but fundamentally because the fruit-bodies are made of hyphae and in ignorance of the hyphal properties the species cannot be defined. The first part of this paper is therefore anatomical. In the second part I have compared the three species—*F. lamaensis*, *F. noxius* and *F. pachyphloeus*—in this detailed aspect, and lastly I have drawn up a description of each for reference. *F. pachyphloeus* I have included, advisedly, because its fruit-bodies have essentially the same construction and are much the easiest to examine and, also, because *F. noxius* resembles it in certain respects rather than *F. lamaensis*, and as both may be parasitic, they too can be mistaken.

The presence of two kinds of hyphae in the fruit-body of *F. lamaensis* has been held to be distinctive, there being stout, thick-walled, dark brown hyphae and slender, thin-walled, more or less colourless hyphae, but I have shown that this is a common feature in the genus (3). I have called it the *dimitic* type of construction, with thick-walled unbranched *skeletal* hyphae and thin-walled branching *generative* hyphae, in *F. levigatus* and *F. senex* which are typical. But there is good evidence for believing that the thick-walled elements in *F. lamaensis* and its allies are not homologous with those of *F. levigatus* and its allies, so that by stating the case differently and with greater precision, the hyphal construction of *F. lamaensis* is found to be distinctive. The thick-walled elements in *F. lamaensis* and its allies I shall call therefore *extrahymenial setae,* in order to distinguish them from the *hymenial* setae, and not skeletal hyphae, and briefly for these reasons, though the full explanation must be deferred until a later paper, when the structure of other species has been described. In true dimity the skeletal hyphae far outnumber the generative hyphae, which lie concealed among them, and they build the stroma. In *F. lamaensis* and is allies, the thick-walled elements play little or no part in the formation and strengthening of the fruit-body: the generative hyphae build the stroma, and the hard agglutinated tissue on the upperside and round the tubes provides the support: the thick-walled elements are merely scattered throughout in inferior numbers and they are always of very limited growth, rarely exceeding half a millimeter in length: in *F. pachyphloeus,* they may appear as seldom as needles strewn in a haystack, the straws of which would be the generative hyphae. Moreover, there are in the dissepiments elements intermediate between the hymenial and extra-hymenial setae which do not exist in cases of true dimity; and there is a species which Lloyd called *F. oroniger* (?=*F. melanodermus* Pat.), which has both incipient skeletals in the flesh like *Polyporus gilvus* and extra-hymenial setae in the dissepiments like *F. pachyphloeus* without there being intermediate states.

Anatomy

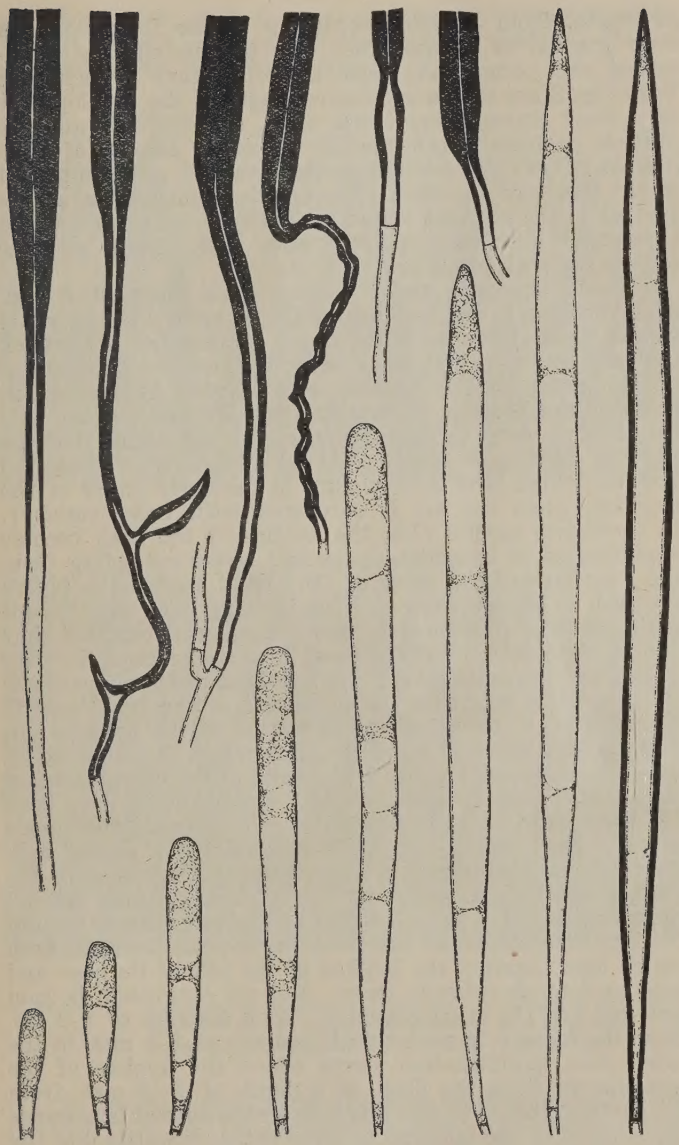
Firstly the process of agglutination must be explained because it takes place extensively in the fruit-bodies of *F. lamaensis* and *F. noxius.* By agglutination is meant the conversion of the primary filamentous tissue into a hard compact mass devoid of air-spaces. Agglutination is often preceded by the development of numerous narrow interweaving hyphae in the tissue but the process really begins with the thickening of the hyphal walls. Then, through some chemical or physical alteration of the surface, the

walls become sticky and fuse together to form a continuous tenacious ground-substance which is riddled by the lumina of the hyphae. As the hyphae gradually adhere, so the air between them is expelled and, in extreme cases, their lumina also disappear and a leathery or stony, structureless substance results. In polypores in which the hyphal walls become yellow-brown in thickening, the ground-substance is also yellow-brown, though macroscopically black, and it acquires a characteristic resinaceous or carbonaceous consistency. Thus, in *F. lamaensis* and *F. noxius*, the dissepiments are very dark brown or black, hard, stony or carbonaceous, and exceedingly difficult to section on account of the agglutination of their tissue: and, in all three species, a stony black crust develops on the upperside of the fruit-body through the agglutination of the superficial hyphae. The nature of the ground-substance I have not been able to determine: like the yellow-brown substance in the hyphal walls, of which it must be a modification, it is turned very dark brown by potash or soda: it is insoluble in weak acids, in weak or strong potash whether hot or cold, in chloroform, ether, xylol, absolute alcohol, and the cellulose-solvents as Schweitzer's reagent and zinc chloride in hydrochloric acid, but it blackens and dissolves slowly in hot conc. sulphuric acid and it disappears rapidly in hot conc. nitric acid: it appears to be impervious to water and once set the hyphae cannot be freed without breaking.

The formation of the fruit-body, the partition of growth at the surface and the direction of the hyphae are exactly as in *F. levigatus* (3), with the distinction that the fruit-bodies are *monomitic, i.e.* are built of equivalent branching generative hyphae. A radial section of the flesh shows the generative hyphae arranged longitudinally with the extrahymenial setae scattered among them, Text-Fig. 1. Most branches of the generative hyphae grow radially but some are interwoven and function as binding hyphae, more especially in *F. pachyphloeus*.

The extrahymenial setae arise terminally from the generative hyphae at the margin of the bracket. The apex of a hypha which is about to form a seta expands gradually or rather suddenly to the specific width of the seta and then in this thin-walled distended state grows on for a variable distance, in some cases for barely 100μ, but never for more than 600μ, and as growth declines so the apex contracts again to some extent. The wall of the distended part may begin to thicken acropetally while apical growth continues, or simultaneously all over on cessation of growth, exactly as in the development of the hymenial setae. The wall is colourless at first but becomes yellow-brown on thickening and finally dark ferruginous, and the lumen is reduced to a line or obliterated. The mediate portions connecting the setae with the generative hyphae vary much

Text-Fig. 1. Radial sections of the flesh of *F. lamaensis* (above) *F. noxius* and *F. pachyphloeus* (below), at ca. 2 cm. from the margin: the sections of *F. lamaensis* and *F. noxius* include one of the dark zones in the flesh, caused by the development and agglutination of numerous interweaving hyphae: × 500.



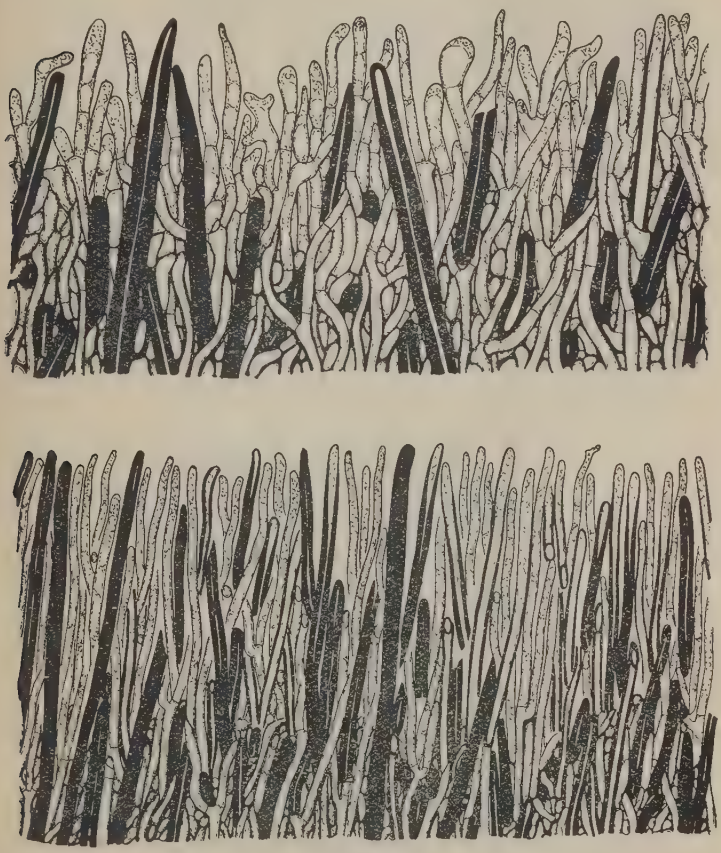
Text-Fig. 2. Stages in the development of an extrahymenial seta at the margin of the pileus of *F. pachyphloeus*, and the proximal and mediate portions of other setae from the flesh: × 500.

in length, from 30–400μ, according as the formation has been gradual or abrupt; they also become slightly thick-walled and occasionally bear a rudimentary branch. In Text-Fig. 2 are shown successive stages in the development of a short extrahymenial seta of *F. pachyphloeus* and the mediate portions of other setae. Thus, on account of their limited growth, the extrahymenial setae are soon immersed in the tissue of the flesh although they must arise at the surface in the growing regions. Their dark brown rod-like appearance and their pointed ends make them striking objects in longitudinal sections.

In *F. lamaensis* and *F. noxius* dark zones, .3–.8 mm. apart, develop in the flesh behind the margin. They stretch as arcs from the tubes to the upper surface and are convex towards the margin. They arise through the rhythmical multiplication of the narrow interweaving hyphae which compact the fibrillar stroma in these limited regions and then become more or less agglutinated. (It seems that the rhythm follows a simple diurnal variation in marginal growth, which is at a maximum in the early hours of the morning when the air is saturated with water-vapour). In these two species also, the hyphae of the flesh become agglutinated in irregular plates and layers extending from the base toward the margin. In radial section the layers are seen as black crustaceous intersecting lines and in some fruit-bodies of *F. lamaensis* they are so numerous that they form a close network at the base: in extreme cases the base of the flesh becomes wholly agglutinated and carbonaceous.

The black crust on the upperside of the fruit-body is preceded by a characteristic formation of the hyphae. In *F. lamaensis* there is initially a pile which is composed of the ends of the generative hyphae and of the extrahymenial setae which have dropped behind the margin and have been deflected more or less perpendicularly towards the upper surface, Text-Fig. 3. It is like the pile of *F. senex* only closer; hence the velvety margin. But it deepens since the hyphae continue to grow out for a short distance behind the margin, and it is compacted at the same time through the intrusion of narrow interweaving hyphae from the flesh which bind together the hyphae of the pile at its base and send up laterals between them. But the outgrowth is soon arrested and the crust develops. At a distance of 1–2 cm. from the margin in young fruit-bodies and 2–5 mm. in the older ones, agglutination starts where the hyphae of the pile emerge from the flesh, at a depth of .2–.5 mm. from the surface, that is to say, and it proceeds outwards towards the surface of the pile and to some extent inwards into the flesh. Thus the crust develops internally from a thin blackish layer just below the upper surface and it grows by extension of the agglutination above and below to form eventually a kind of carbonaceous rind. Macroscopically,

the rich brown subtomentose zone near the golden-yellow velvety margin gives place to a dull black glabrous surface with the leaden aspect of asphalt.

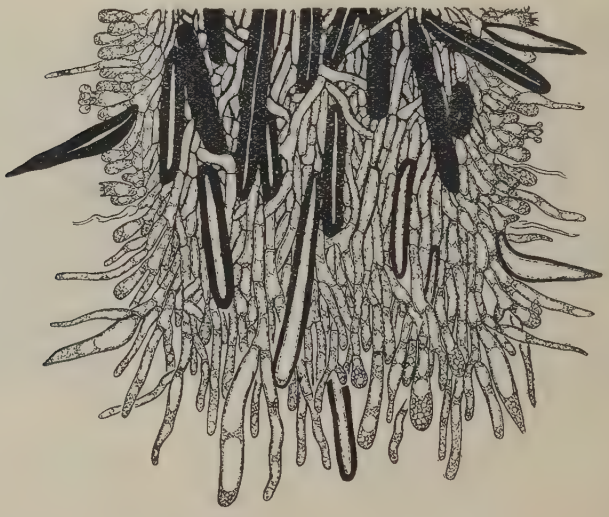


Text-Fig. 3. Sections of the upper surface of the pileus of *F. noxius* (above) and *F. lamaensis* (below), at 4 mm. behind the margin of young actively growing fruit-bodies: × 500.

In the other two species the crust develops in essentially the same way but the preliminary pile is indistinct because the generative hyphae are wider and, as they are crowded together behind the margin, they are compacted to form a pseudoprosenchymatous tissue, Text-Fig. 3: the cells, also, which are cut off by the outgrowing generative hyphae in

the pile are short and scarcely filamentous. Agglutination begins at an early stage and very much nearer to the surface, often only 20–30μ below the ends of the hyphae, but the outgrowth of these ends lasts longer and thus the crust is thickened. The extrahymenial setae often project further than in *F. lamaensis*, up to 350μ in a variety of *F. pachyphloeus*, but they are overgrown eventually by the generative hyphae in most cases, just as in *F. levigatus*: (it is probable that, as in that species too, the more salient setae in *F. pachyphloeus* are secondary and derived from the excrescent generative hyphae). Macroscopically therefore, the surface of the pileus just behind the margin tends to be coarsely velvety or minutely hispid in these two species and it is more rapidly glabrescent. The section, drawn in Text-Fig. 3, would serve as well for *F. pachyphloeus*, except for the lesser width of the extrahymenial setae.

The mature crust in all three species has the same appearance. In thin sections it is a yellow-brown homogeneous resinaceous layer in which occasionally the vestiges of the hyphal lumina can be seen as a faint mottling, or the darker blurrs of the agglutinated setae.



Text-Fig. 4. A longitudinal section through the growing end of a dissepiment of *F. lamaensis*: × 500.

The dissepiments, except that they are built from generative hyphae, like the flesh, arise in the same way as in *F. levigatus*. But in *F. lamaensis* and *F. noxius* the tissue on the lower side of the pileus becomes agglutinated

at a distance of 1–4 mm. from the margin, before the pores are delimited. The excrescent hyphae of the pore-field, that is, become agglutinated exactly as those on the upperside of the pileus in *F. noxius*: in fact, if the upper figure in Text-Fig. 3 were inverted it would serve for the pore-field of *F. noxius*, or *F. lamaensis*, were the hyphae narrower. Agglutination begins about 50μ above the ends of the downgrowing hyphae, but soon approaches within 20–40μ. A thin crust, ca. 70μ thick, thus forms internally in the pore-field above the thin-walled hyphal ends and from the crust will depend the tubes. Partition of growth in the pore-field gives rise to the dissepiments, and the downgrowing hyphae of the dissepiments continue to become agglutinated about 20–40μ above their ends so that only the terminal cells are really free. The subterminal cells which are cut off are short, also, and about 10–30μ long, as on the upperside of the pileus in *F. noxius*. How rapidly the tissue is consolidated can be gathered from Text-Fig. 4. In these two species, therefore, the dissepiments are darkly coloured, hard and carbonaceous, brittle to the razor, and this property distinguishes them at once from *F. pachyphloeus* in which the hyphae are not, or only very slightly, agglutinated in the dissepiments, these having the same light fibrillar texture as the flesh, Text-Fig. 6. It is remarkable, indeed, that the downgrowing hyphal ends in *F. lamaensis* and *F. noxius* can obtain any nourishment through such a mass of agglutinated tissue, for the dissepiments may reach several millimetres in length.

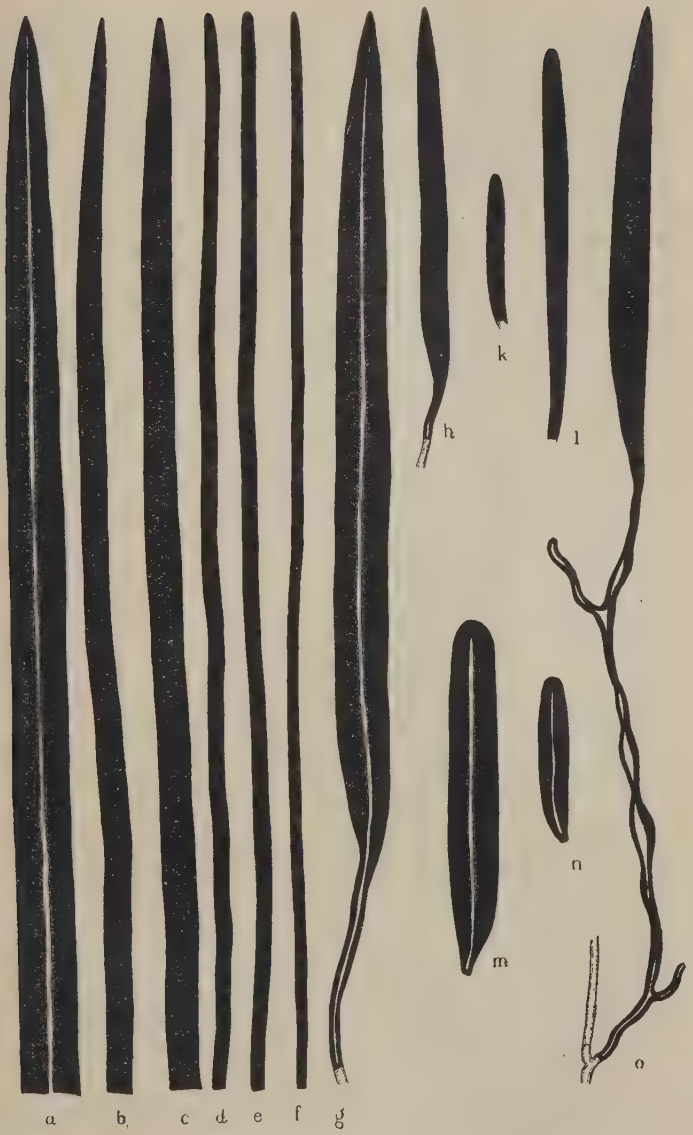
The hymenium is developed sympodially from the ends of the hyphae which are arrested in growth and lie along the flanks of the dissepiments. On the free side of their ends the wall is bulged out at right angles into the tube and the bulge develops into a cystidium or, in some cases, a seta. This primary bulge is cut off by a septum and basidia and setae develop from below by sympodial branching. The subhymenium is only 1–2 cells thick and the cells are 6–10μ long by 2–3μ wide. The hymenium, thus built up, is compact but ephemeral. The cystidia very soon collapse, being found only near the pores, and the hymenium itself is fertile only for a distance of 1–3 mm. from the pores in *F. pachyphloeus* and *F. noxius*, and for barely .5 mm. in *F. lamaensis*. When exhausted, the hymenium is replaced by a 'false hymenium.' The basidia, being thin-walled, collapse on to the subhymenial hyphae which develop slightly thickened, slightly agglutinated, pale yellowish walls, and the obtruncated ends of the subhymenial hyphae persist as an 'epithelium' or 'false hymenium' with a peculiar pavement-like appearance, Text-Fig. 6. It covers all but the extremities of the dissepiments and would be mistaken for the true hymenium, were its nature not proven developmentally.

The extrahymenial setae in the dissepiments arise among the free ends of the downgrowing hyphae, like those of the flesh at the margin of the pileus: they do not develop subterminally in the tissue though subsequently on account of their limited growth they are embedded. Characteristically, in all three, they are much more limited than in the flesh, Text-Fig. 5. In *F. pachyphloeus* they may reach 300μ in length; in the other two they do not exceed 100μ. This limitation results merely from the fact that the generative hyphae have shorter cells on the average in the dissepiments than in the flesh, and the extreme limitation in *F. lamaensis* and *F. noxius* is the outcome of agglutination. The extrahymenial setae are only apical cells bodily modified. They are not special hyphae, *i.e.* elements of unlimited growth, and their lengths correspond exactly with those of the apical cells. In the flesh the cells of the generative hyphae vary 80–400μ in length: the apical cells are roughly twice as long and so are the extrahymenial setae with their mediate portions. In the dissepiments of *F. pachyphloeus* the cells of the generative hyphae vary 40–180μ long; in *F. noxius* and *F. lamaensis* they are 10–40μ long, for when the hyphae are agglutinated close to their growing points their apical cells divide much more frequently and their constituent cells are therefore much shorter: the extrahymenial setae in the dissepiments of these two species are therefore very limited. (This metrical agreement between the extrahymenial setae and the single cells of the generative hyphae is one of the most cogent reasons for distinguishing them from the skeletal hyphae of *F. levigatus*, which are essentially elements of unlimited growth).

The hymenial setae develop as in *F. levigatus*. Their primordia are subclavate cells indistinguishable from the young basidia, but the free ends of the primordia soon begin to protrude in a blunt process which narrows as it extends and thus, on cessation of growth, gives the acute apex to the seta. On reaching full-size the wall thickens simultaneously all over or with a slight acropetal tendancy from the base. The hymenial and extrahymenial setae both develop in the same way as modified apical cells. They are homologous. But the hymenial setae are very short because with all the other cells of the hymenium they are of very limited growth and, like those cells also, they are directed at right angles to the longitudinal extrahymenial setae.

The cystidia develop like the setae but they never become thick-walled. They appear to be setae which are limited not merely in growth but in differentiation. The development of both can be seen in Text-Fig. 4.

Elements intermediate between hymenial and extrahymenial setae are naturally to be expected. When the hyphal end which is about to form a thick-walled element



Text-Fig. 5. Extrahymenial setae of maximum and minimum sizes: *a*, *b* from the flesh and *g*, *h*, *o* from the dissepiments of *F. pachyphloeus*: *c*, *d* from the flesh and *m*, *n* from the dissepiments of *F. noxius*: *e*, *f* from the flesh and *k*, *l* from the dissepiments of *F. lamaensis*: × 500.

is situated at the edge of the dissepiment neither on the flank nor yet at the apex, the resulting seta is short and subventricose and it projects obliquely into the tube: in length, shape and direction it is intermediate. Such elements are common in *F. pachyphloeus* (Text-Fig. 8), but rare in *F. lamaensis* and absent from *F. noxius* which has no hymenial setae, this being its prime condition. The two kinds of seta in *F. pachyphloeus* and *F. lamaensis* show very clearly how intricate are the factors which govern the behaviour of the hyphae in the fruit-body. Some hyphal apices have a propensity for becoming setae, *i.e.* thick-walled cells; the kind of seta which they will become depends in the dissepiments on whether they lie within or without the influence of the form-factors of the hymenium, which may be a matter of a space of 4 or 5μ or less.

A conspicuous feature, though one by no means peculiar since it is found in many other species of Fomes and Ganoderma, is the presence of white floccose strands radiating from the base to the margin in the flesh of old fruit-bodies. They are incursions from the mycelium and they are composed of two kinds of hyphae. There are many narrow, much branched, lobed and interwoven hyphae, 2–6μ wide, which become slightly thick-walled, and a few large thin-walled radiating hyphae with inflated cells, 6–18μ wide, which appear as storage elements. At first the narrow hyphae grow in singly between the hyphae of the flesh around which they apply themselves very closely and then gradually corrode away their thickened walls. The narrow hyphae thus lead the way, softening and eating out the tissue, and only later do the white strands develop in tunnels so excavated. The narrow hyphae penetrate also into the tubes where they form a white or pale yellowish wadding, as in *F. levigatus*. They apply themselves closely to the remains of the subhymenium and round the ends of the setae the walls of which are also very slowly dissolved. But the carbonaceous tissue of the dissepiments and the crust on the pileus are too dense to be affected.

Just as in the starved fruit-bodies of *Polystictus xanthopus* (2), the walls of the hyphae are corroded from the outside towards the lumen, (which suggests that it may have been the generative hyphae which ate away the skeletals in *P. xanthopus* too). The hyphae of the flesh are rendered very thin-walled and tenuous and ultimately they disintegrate. The generative hyphae naturally disappear first and the extrahymenial setae more slowly. So, in an intermediate stage, the extrahymenial setae lie free in the loose mass of intrusive hyphae in the disintegrated stroma and they can easily be teased apart under the microscope, especially in *F. pachyphloeus;* in fact, this half-digested tissue is the most suitable for studying the extrahymenial setae.

The process is a kind of autodigestion, but to what end it is difficult to discover, unless the narrow hyphae which penetrate deeply into the fruit-body can carry the products of digestion to the growing hyphae at the margin and at the ends of the dissepiments. It seriously interferes with the enlargement of the fruit-body on the original stroma, which is the Fomes-mechanism, because the flesh may be changed completely into a loose felt and the fruit-body, thus deprived in great measure of its support, may drop off: the flesh may be consumed to such an extent that the crust is detached for a distance of several centimetres from the base. It seems, however, that the fungus cannot prevent these cannibalistic excursions from the mycelium.

In *F. lamaensis* many of the white strands are enclosed in black crustaceous tubes, suggesting that the hyphae of the flesh immediately surrounding the strands become agglutinated to stop any further intrusion. These crustaceous layers are very seldom formed in the flesh of *F. pachyphloeus* and its fruit-bodies suffer the more.

Specific Comparison

The three species agree in the following respects:—

Habitat: lignicolous, tropical.

Mycelial characters: forming brown or blackish intersecting lines in the infected wood, often as an irregular network.

Fruit-bodies: typically sessile, applanate, perennial brackets; upperside sulcate, brown and velutinate at the margin, becoming glabrous and dull black; margin obtuse; flesh thick, yellow-brown, with a thick black stony crust on the upperside and ultimately traversed by white mycelial strands increscent from the base; tubes unlimited; pores minute, round, ca. 100μ wide; dissepiments 40–100μ thick.

Hyphal structure of the fruit-body: monomitic with extrahymenial setae, not exceeding 600μ long, having thick yellow brown walls and pointed ends; generative hyphae unclamped.

Spores: white, broadly ellipsoid, smooth, thin-walled, 1-guttate, ca. $4 \times 3\mu$.

Basidia: ca. $10 \times 4\mu$, with 4 sterigmata ca. 2μ long.

Cystidia: thin-walled, hyaline, subventricose, 1.5–4μ wide.

Hymenium: ephemeral.

They differ in the following respects:—

F. lamaensis.	*F. noxius.*	*F. pachyphloeus.*
Fruit-bodies often effuso-reflexed, rarely resupinate; pilei applanate.	Effuso-reflexed, often resupinate; pilei applanate.	Rarely effuso-reflexed; pilei becoming ungulate.
Upperside initially deep rich brown.	As *F. lamaensis.*	Initially light fulvous.
Growing margin pale fulvous-ochraceous.	White or cream-colour.	Light fulvous.
Growing pores umber with a grey bloom.	As *F. lamaensis.*	Light fulvous-cinnamon.
Flesh hard, dense, woody; 2.5–10 mm. thick at the base, rarely up to 5 cm. thick, with dark brown, narrow zones and numerous intersecting black crustaceous layers.	As *F. lamaensis.*	Very thick, light, fibrous-woody; 12–130 mm. at the base; without zones and rarely with a few crustaceous layers.
Tubes in the first season up to 10 mm. long, finally up to 26 mm. long.	Up to 5 mm. and 11 mm. respectively.	Up to 24 mm. and 175 mm. respectively.
Dissepiments carbonaceous with agglutinated hyphae.	As *F. lamaensis.*	Fibrous with the hyphae not, or only slightly, agglutinated.
Pores 110–130μ wide.	80–110μ.*	55–100μ.
Extrahymenial setae in the flesh 3–5μ wide.	4–10μ.*	8–17μ.
Extr. setae in the dissep. up to 100μ long × 5–7μ wide, abundant.	Up to 100 × 9–16μ,* much less abundant.	Up to 300 × 9–17μ, abundant.
Hyphae of the flesh 2–3.5μ wide.	2.5–5μ.*	1.5–5μ.

Table of Differences.—*contd.*

F. lamaensis.	*F. noxius.*	*F. pachyphloeus.*
Hymenial setae very abundant, 5 – 8μ wide.	Absent.	Abundant, 4–10μ.
The pile on the upperside long persistent.	Soon agglutinated.	As *F. noxius.*
Spores 3–3.5 × 2.5–3μ.	3.5–4.5 × 3–3.5μ.*	4–6 × 3.5–4.5μ.
Mycelium forming superficial brown felts.	As *F. lamaensis.*	?
Saprophytic.	Frequently parasitic.*	As *F. noxius.*

Some of these points are worth expounding.

The fruit-bodies of *F. noxius* are the least typical of the genus. They are degenerate and tend to the resupinate condition of Poria. A resupinate patch is always developed before the pilei project horizontally; even on vertical surfaces, patches up to 12 cm. in extent precede the pilei. Those of *F. lamaensis* and *F. pachyphloeus,* on the other hand, are typically sessile brackets. On vertical surfaces their primordia are hemispherical knobs, as compact as can be, and they grow directly into the brackets, like those of *F. levigatus*: subsequently, in *F. lamaensis,* a small resupinate 'foot' is usually developed by a limited spreading of the lower margin of the primordium. Only when the primordia of *F. lamaensis* arise on the underside of branches do they form extensive resupinate patches like those of *F. noxius,* and when the margins of these patches begin to ascend the sides of the branch they grow out into flange-like pilei. I have found very few fruit-bodies of *F. pachyphloeus* of this effuso-reflexed form, which is so common among sessile polypores, probably because it grows mostly on upright trunks, living or dead: however, it certainly has not the spreading Poria-tendancy of the other two.

The fruit-bodies of *F. lamaensis* and *F. pachyphloeus* may reach a large size, one of *F. pachyphloeus* being among the largest recorded for the polypores. But while those of

F. lamaensis are always relatively thin, those of *F. pachyphleous* thicken and become more or less ungulate, as massive tube-layers develop each season with the minimum of sterile tissue at the margin. In *F. lamaensis,* the hymenium is extended perennially by the marginal growth of the pileus rather than by the downgrowth of the dissepiments; in *F. pachyphloeus,* by downgrowth of the dissepiments rather than by marginal growth of the pileus. The difference can be referred directly to the structure. The agglutination of the dissepiments in *F. lamaensis* must interfere with the food-supply to the downgrowing hyphal ends; they cannot deflect the food from the mycelium so strongly as those in *F. pachyphloeus* which are not impeded by agglutination. Therefore, the food goes mostly to the margin in *F. lamaensis.* In *F. pachyphloeus* the food, travelling radially, can be drained away vigorously all along into the dissepiments and little will arrive at the margin, which is consequently stunted.

The fruit-bodies of *F. noxius* are much smaller and this is doubtless due to the fact that it frequents opener places where growth is more likely to be interrupted by spells of dry weather. Apart from cultivation, I have found *F. noxius* only in secondary jungle or in clearings in the forest, and the largest specimen I gathered in an overgrown thicket at the edge of a ricefield near Kuala Pilah, Negri Sembilan. I have never found *F. lamaensis* in the open, but seldom in secondary jungle, nearly always and always most luxuriantly in the damp riverside forests on the well-rotted tree-trunks. *F. pachyphloeus,* in the same way, seems to develop best when parasitic on the big trees in the high forest.

The different texture of the flesh is due to the differences in size and relative abundance of the two kinds of tissue-elements, which can be seen in Text-Fig. 1. The tissue is densest in *F. lamaensis* because the elements are the narrowest and the extrahymenial setae are relatively most abundant. It is lightest in *F. pachyphloeus* because the relations are inverted, the extrahymenial setae being relatively the least numerous and the generative hyphae the widest. *F. noxius* is intermediate.

The chief points in which *F. noxius* is intermediate between the other species are indicated in the Table of Differences by an asterisk. They relate to the width of the tissue-elements, but it is unwise to suppose that *F. noxius* is phylogenetically a link between them. The similar structure of the upper surface in *F. noxius* and *F. pachyphloeus,* which is suggestive at first sight, is probably only an outcome of the greater width and preponderance of the generative hyphae accompanied with early agglutination, as in the pore-field also of *F. lamaensis,* as well as in *F. noxius.* As already mentioned, *F. lamaensis* and *F. noxius*

are easily distinguishable from *F. pachyphloeus* by the agglutinated tissue of their dissepiments.

The surest way to distinguish *F. lamaensis* from *F. noxius* is by a longitudinal section of the dissepiments; it is most unsafe to rely on macroscopic characters. In the section from *F. lamaensis*, numbers of hymenial setae will be seen projecting perpendicularly into the tubes besides the ends of the extrahymenial setae which lie obliquely near the surface, Text-Fig. 6. In *F. noxius* there are only the ends of the oblique extrahymenial setae, which are two or three times as wide as those of *F. lamaensis* and far less numerous, Text-Fig. 6: one may need to search in several tubes, indeed, before finding any, whereas the least fragment of *F. lamaensis* from which a section can be cut will discover both kinds. But, to be quite clear, let me repeat the characters of the hymenial setae. They are thick-walled apical cells *in the hymenium;* their long axes are therefore at right angles to those of the hyphae in the dissepiments; they are more or less conical, subventricose below, with acute apex, and they rarely exceed 40μ long. In all the fruit-bodies of *F. noxius* which I have examined, I have seen nothing of the kind.

The alternative distinction in the width of the hyphae is not as certain, although it holds in most cases. I have a few collections in which the hyphae are about as wide as in *F. noxius*, but I prefer to regard them as a variety of *F. lamaensis*, as will be explained later. They do not upset the identification of the Brown-root fungus because they are not parasitic.

Specific Descriptions

Fomes lamaensis (Murr.) Sacc. et Trott. Sacc. Syll. Fung. 8.

Syn. *Pyropolyporus lamaensis* Murr. Bull. Torr. Bot. Club 34, 479, 1907.

Pyropolyporus Williamsii Murr. Bull. Torr. Bot. Club 34, 479, 1907.

Fomes Williamsii (Murr.) Sacc. et Trott. Sacc. Syll. Fung. 8, 289.

Fomes Williamsii (Murr.) Bres. Hedw. 53, 59, 1912,

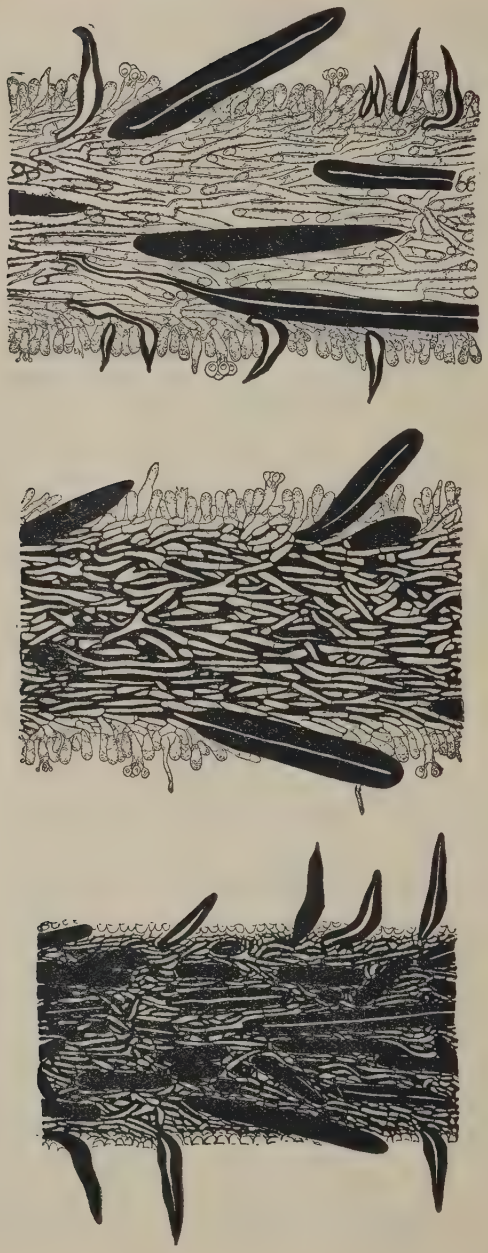
Fomes lamaoensis auctt.

? *Fomes* (Poria) *cacao* Pat.

? *Fomes sublamaensis* Lloyd

Effuso-reflexed, or sessile, bracket-shaped with a more or less distinct resupinate foot, rarely wholly resupinate: pilei dimidiate, applanate, often subspathulate and lobed in large specimens, *ascending*, sometimes imbricate, up to 28.5 cm. in radius, 43 cm. wide: effuso-reflexed specimens with the resupinate part spreading up to 30 cm. wide, and the pilei fusing into horizontal flanges.

Upperside *concentrically sulcate* with narrow crowded zones or broad distant zones, *more or less velutinate*, sometimes matt, *deep*



Text-Fig. 6. Longitudinal sections of the dissepiments; a, *F. lamaensis*; b, *F. noxius*; c, *F. pachyphloeus*: × 100.

rich brown, tawny-bay, *becoming glabrous and blackish brown* from the centre outwards, often with narrow darker zones, *finally wholly glabrous and dull pitch-black*: *margin* obtuse, becoming lobed in large specimens, subvertical and shortly stepped in perennial forms, *pale tawny-ochraceous*, darker when dry.

Flesh mostly rather thin 2.5–10 mm. thick at the base and .5–8 mm. thick at 5 mm. from the margin, occasionally up to 5 cm. thick at the base and 10–19 mm. at 5 mm. from the margin, .5–2 mm. thick in the resupinate part, *woody*, dense, rigid, rather sappy when young, *varying bright tawny-ochraceous to dark cinnamon-ferruginous* with narrow crowded darker zones, *developing a carbonaceous black crust*, .5–2.5 mm. thick, *on the upperside and black radiating carbonaceous plates and lines*, .5–1.5 mm. thick, *in the tissue*, often intersecting to form a network: *finally with white floccose mycelial strands radiating from the base.*

Tubes rather short, in the first season up to 10 mm. long at the base and .3–2 mm, at 5 mm. from the margin, in perennial specimens with several layers each 1–10 mm. thick and often separated by a thin layer of flesh .3–1 mm. thick, giving a total thickness up to 26 mm., *stony or carbonaceous*, *umber*, drying datebrown or fuscous: *pores umber with a grey bloom*, drying date-brown, round, *minute*, 110–130μ wide. with dissepiments entire, 40–100μ thick.

Spores 3–3.5 $\times$ 2.5–3μ, *white*, broadly ellipsoid, thin-walled, with one small gutta, .5–1μ wide.

Basidia 8–11 $\times$ 3.5–4μ subclavate, with 4 sterigmata, 1.5–2μ long.

Cystidia 16–130 $\times$ 1.5–4μ wide below and 1–1.5μ wide above, ventricose, apex gradually tapered, thin-walled, colourless, vacuolate, evanescent.

Hymenial setae 20–45 $\times$ 5–8μ, conical or subventricose, apex acute, rarely obtuse, straight or slightly curved, very thick-walled, more or less solid, dark ferruginous, smooth, *very abundant.*

Extrahymenial setae up to 600μ long $\times$ 3–5μ wide in the flesh, up to 100μ long $\times$ 5–7μ wide in the dissepiments, *abundant.*

Generative hyphae 2–3.5μ wide.

Hab. in damp forest, saprophytic on tree-trunks.

EXSICCATI EXAMINED:—

Type-collection of *F. lamaensis*, Lamao R., Luzon, P. I., Nov. 1904, R. S. Williams.

Type-collection of *F. Williamsii*, Lamao R., Luzon, P. I., Dec. 1903, R. S. Williams.

Bur. Sci. Man. No. 50131, P. I., 1931, C. J. Humphrey.

Bur. Sci. Man. No. 50132, P. I., 1929, C. J. Humphrey.

Sing. Field No. 5094, Singapore, 1919, T. F. Chipp.

Sing. Field No. 5377, Singapore, 1919, T. F. Chipp.

Sing. Field No. 5876, Singapore, 1920, T. F. Chipp.

Sing. Field No. 5878, Singapore, 1920, T. F. Chipp, named *F. senex* Mont. by C. G. Lloyd.

Sing. Field No. 9462, Johore, 1922, R. E. Holttum.

Sing. Field No. 9507, Johore, 1922, R. E. Holttum.

Sing. Field No. 9510, Johore, 1922, R. E. Holttum.

Sing. Field No. 10950, Johore, 1923, R. E. Holttum, named *F. extensus* Lev. by C. G. Lloyd.

Sing. Field No. 23712, Negri Sembilan, 1930, E. J. H. Corner.

Sing. Field No. 24490, Negri Sembilan, 1930, E. J. H. Corner.

Sing. Field No. 24487, Pahang, 1930, E. J. H. Corner.
Sing. Field No. 24488, Pahang, 1930, E. J. H. Corner.
Sing. Field No. 12190, Kelantan, 1924, M. Nur.
Sing. Field No. 19014, Borneo, 1927, C. Boden-Kloss.
Sing. Field No. 19192, Borneo, 1927, C. Boden-Kloss.
Sing. Field No. 14589, Sumatra, 1924, C. Boden-Kloss.
C. F. Baker No, 5408, Singapore, 1917, named *Fomes* (Poria) *cacao* Pat. by N. Patouillard. ? co-type.

That it is the true *F. lamaensis* and that *F. Williamsii* is a synonym, as Bresadola first noted, I have checked by microscopic examination of the types. Both types are in the herbarium at the New York Botanic Gardens and were collected by R. S. Williams on the Lamao River, P.I. They were described by Murrill in the same paper and on the same page in terms that are almost identical, though Murrill seems not to have noticed any similarity, and in the next year he assigned *F. Williamsii* to *F. endothejus* Berk. (7), which, as Bresadola and Lloyd have remarked, is utterly false since *F. endothejus* is a species with brown spores and without setae. The description of *F. lamaensis* came first and this name therefore has priority. Bresadola substituted the name '*Williamsii*,' in which he was followed by Patouillard, apparently on the ground that the fruit-bodies in the type-collection of *F. Williamsii* being larger than those in the type-collection of *F. lamaensis* represented what he called the 'status adultus,' those of *F. lamaensis* being the 'status juvenilis' of the species. But this notion seems to have arisen from a remarkable misunderstanding. In the first place, the term 'adult' cannot be applied to fruit-bodies of the Fomes-kind which are virtually of unlimited growth and which continue to produce basidiospores from a very early stage, unless it is reserved for those fructifications which do produce basidiospores and so must then be applied to every state but the primordial knob, in which case the terms 'mature' and 'immature' seem more appropriate. But the fruit-bodies in the type-collections of both species are all mature, though in neither can they be regarded as full-grown since the fruit-bodies are perennial and much larger ones are easy to find elsewhere. In the second place, it seems that the terms 'status juvenilis' and 'status adultus' (which can mean only immature and mature) were confused with the terms 'imperfect state' and 'perfect state' in their mycological sense and thus the rule of procedure for the radically different proposition when a *fungus imperfectus* is joined with an ascomycete or basidiomycete was applied here also. It is important that this point should be clear or it may become lawful to substitute many other names for the singular reason that they were given to bigger specimens of the same species.

The species name, taken from the place of discovery,

Lloyd changed to 'lamaoensis,' which etymologically may be the more correct, and he has been followed by others. But one must keep to the original spelling as it is clearly no misprint. The origin of the name 'Lamao' is, moreover, uncertain. Is it a native word, or is it derived from the spanish 'lama' meaning 'mud' or 'flat swampy land' (latin, lama-ae), or, as seems most likely, from 'la maño,' meaning the hand, which has suffered contraction and fusion into 'lamao,' for there is also a Point Lamao?

Lloyd has explained the late discovery of this species which is so common in the East (6). It was mistaken for *F. igniarius*. In the herbarium at Leiden he found many collections which had been sent from Java nearly a hundred years ago and thus referred.

The collection named *Fomes cacao* Pat., listed above, may be part of the type but I have not access to the original description and cannot be certain if the name is a synonym. Baker wrote on the packet in the Singapore herbarium '*Fomes* (Poria) *cacao* Pat. n. sp.' and it is evidently a collection which he made in the Singapore Botanic Gardens and sent to Patouillard for identification. It is merely an ill-developed resupinate form of *F. lamaensis;* the conditions in the Botanic Gardens are now too dry for the growth of this species.

There is no reliable evidence that this species is ever parasitic. It is a common saprophyte in the Malayan forests from sea-level to an altitude of 4,000 ft. (Fraser's Hill); whether it occurs on the highest mountains cannot yet be said, for they have not been explored mycologically.

The shape of the fruit-body is characteristic. Commonly marginal growth is so strongly ascending that a rather thin, rigid bracket with strongly concave upper surface and convex under surface is produced and such fruit-bodies, seated like wall-basins on the tree-trunks, can easily be recognised from afar, as shown in the Plate.

Spores are few because the hymenium is limited to a distance of 500μ at most from the pores and it is not very active. In spite of many attempts I have not obtained a spore-print, though microscopic examination has afterwards revealed fertile basidia scattered through the hymenium. If the spores are so scarce, why is this species so abundant? Like those of *F. levigatus,* and of *F. noxius* and *F. pachyphloeus* also, the fruit-bodies cannot survive even a few days desiccation once detached from the substratum; they merely become very mouldy on soaking out again. Even when attached to the substratum, they will spore again after desiccation only when new hyphae have grown out from the margin and dissepiments and formed a new hymenium; they have no means of interstitial growth in the old hymenium and are thus in striking contrast to the Polystictus-type.

In two respects the fruit-bodies are so variable that it might seem advisable to distinguish varieties. Most obvious are differences in the appearance of the upper surface, which may be velvety or tomentose for a distance of several centimetres from the margin or only finely velutinate or matt, initially, and rapidly glabrescent: and there are many intermediate states. But specimens of any one collection from the same piece of wood, and therefore developing, presumably, from the same mycelium, always agree in their state of velvetiness, which must be hereditary. But what is meant by this velvetiness? It is a macroscopic character which signifies a palisade of free hyphal ends at the surface, what I have called the pile on the upperside. Now the pile has two obvious properties, the one of height, the other of extent, both of which effect the macroscopic velvetiness. Take, first, the height. It is determined primarily by the outgrowth of the hyphae after they have quitted the margin, which, if long continued, results in a tall pile and a velvety surface and, if soon arrested, a low pile and a matt surface. But it is also determined by the depth below the surface at which the crust develops, *i.e.* the distance between the ends of the hyphae on the upper surface and the level in the flesh where their stalks begin to be agglutinated, for this distance being the free length of the hyphae is the height of the pile. The distance is generally 100–200*u*, but in some cases only 50*u* and in others as much as 500*u*, which is a range easily sufficient to cover the terms matt to tomentose as they are used in mycology. The height of the pile is thus the result of two independant processes and different combinations of the two may have the same effect. For example, a thickly velvety surface may result from a long-continued outgrowth and a crust beginning at a medium depth of 200*u*, or from an early arrest of outgrowth and a crust beginning at the greatest depth of 500*u*: similarly, a matt surface will result when the crust begins at a shallow depth whether or not the outgrowth is long-continued. In practice, however, it is often exceedingly difficult to determine how these processes have been combined because there is no base-line of reference in the fruit-body. Some simple cases are shown in Text-Fig. 7. Specimens *a* and *d* both have the outgrowth on the upper surface long-continued, as can be told in the radial section from the descent of the upperside toward the margin, c.f. the ascent of the pores on the underside. But in specimen *a* the crust develops deeply so that the surface is tomentose and in specimen *d* it develops very near to the upper surface which is matt. Contrast, then, specimens *b* and *e*. The outgrowth in both is soon arrested, since the line of the upperside runs parallel with the direction of marginal growth, which is ascending, but specimen *b* is tomentose because the crust develops deeply and specimen *e* is only

velutinate because the crust develops nearer to the surface. Thus specimens *a* and *b* are both tomentose but for different reasons and specimens *d* and *e* are both matt, also, for different reasons (the crust develops much nearer to the surface in *d* than in *e*). Specimen *c* is rather a freak, but it shows how important is the level of inception of the crust.

Take now the extent of the pile. How much of the upper surface behind the margin will be velvety? It depends upon the rate at which the pile is effaced through the development of the crust and, also, upon the rate of marginal growth. The rate at which the pile is effaced depends in turn on three factors, at least:—

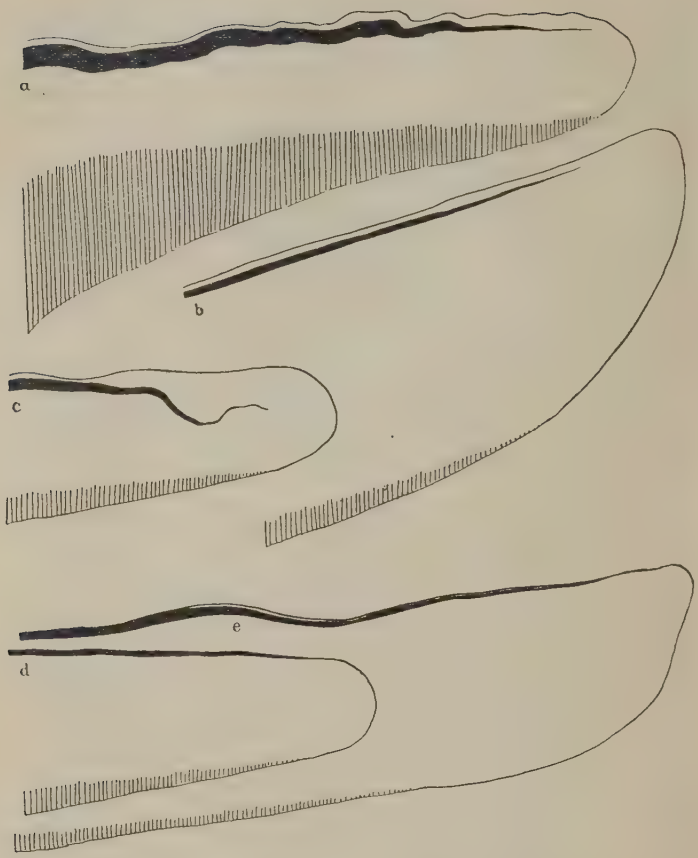
a. on the rate of agglutination in the tissue: (it may proceed at 1μ an hour, or double or treble or half this rate, for who knows?): if low, the pile will remain free for a long time and the surface will tend to be widely velvety.

b. on the rate of outgrowth of the pile: if a high rate is maintained for a long time, then it will be longer before the crust reaches the surface than if the rate were low or the time were short, and the surface will tend to be widely velvety.

c. on the level of inception of the crust: if deep, then the crust will take longer to reach the surface than if shallow, and the surface will tend to be widely velvety.

There are no data on these points and they will be exceedingly difficult to obtain, yet without them one cannot analyse completely the state of the upper surface from mere inspection. As for the rate of marginal growth, it is obvious that when it is high there will be a wider zone occupied by the pile between the margin and the mature encrusted surface than when the rate is low. The rate is highest in young fruit-bodies and declines as the fruit-bodies grow older. Small fruit-bodies, which are young, tend therefore to have a widely velvety surface and large ones, being old, tend to have only a narrow velvety zone, 1–2 mm. wide, near the margin. But not all fruit-bodies are small because they are young. Many are small because they are stunted through lack of food or lack of moisture, or because they have developed in rather dry surroundings which have reduced the rate of growth continuously or intermittently in spells of dry weather, and the macroscopic appearance of the upper surface varies accordingly. So the extent of the pile is determined by many independant factors different combinations of which give the same effect, just as in the case of the height of the pile.

Evidently 'velvetiness' is no simple character which can be used as an element in classification but a most complicated one derived from the interaction of environmental factors as well as numerous internal form-factors. A variety 'tomentosus' would mean an unnatural assemblage of young or stunted fruit-bodies, some with deeply conceived



Text-Fig. 7. Radial sections through the margins of actively growing pilei of *F. lamaensis*: the thick line below the upper surface represents the crust: × 5.

crust, some with long-continued outgrowth of the pile, some with slow agglutination and so on. Velvetiness is a phenotypic character. The hereditary genotypic characters are the states of the form-factors and on them varieties should be based: but I have refrained because it is too difficult to determine them.

In the second place there is the colour of the flesh, which is generally bright tawny-ochraceous, in some cases lurid ochraceous, but in others dark ferruginous; in some it is the colour of turmeric, in others the hue of mahogany: and there are all intermediate states. The difference in

some cases is merely one of age, the colour darkening as agglutination proceeds in the old fruit-bodies. In other cases it appears to be hereditary, like the states of velvetiness, some fruit-bodies having the darkly coloured flesh from the first. Such fruit-bodies with dark flesh Lloyd made into a new species, *F. sublamaensis* (5). Now the colour of the flesh depends upon the thickness of the hyphal walls, the size of the hyphae, the abundance of the extrahymenial setae, the closeness of the tissue, the degree of agglutination, the intensity of the pigment on the wall, in the wall and in the lumen, and on the amount of moisture present, to cite but a few possibilities. These are independant factors, different combinations of which may have the same macroscopic effect and these effects are also exceedingly difficult to analyse in practice. What good can come of confusing them by basing a variety or a species on the character 'brownness,' which unqualified has no mycological significance? What is it that is brown? Add to which the induction that a very slight, imperceptible variation in one determining factor in the individual hypha may make an appreciable difference macroscopically when thousands are viewed together in the mass. The shade of the flesh may be determined by differences which are trifling in the living units. Furthermore, fruit-bodies with the flesh of one shade may have matt or tomentose surfaces: the colour of the flesh and the velvetiness of the surface do not vary together. How can one classify the combinations of these two characters, let alone analysing each in its causal aspect? Confusion surely must result from using such macroscopic characters in mycological systematy, unless they indicate unmistakeable hyphal properties.

I have gone into these variations at length because they offer in the extreme such striking differences, or some will affirm that I have confounded several species as *F. lamaensis*. Velvetiness and colour of the flesh are favourite diagnostic characters, but as they mean so much they are useless till qualified microscopically. Almost all the muddles and mistakes—and many there are too—in the systematy of polypores have arisen through this reliance on macroscopic characters without analysing them, and the microscopical elements have been overlooked from which one can identify with certainty. It must be right to deal at first with hyphae, not hairs or down, or velvet or tomentum, which are compound.

Fomes lamaensis var. **secedens** var. nov.

A forma typica differt setis extrahymenialibus paulo crassioribus, in carne 4–8μ latis, in dissepimentis 5–9μ latis, et hyphis generantibus 2–4.5μ latis.

Type:—Sing. Field No. 24489, Pahang (Padang Piol), 1930.

EXSICCATI EXAMINED:—

Sing. Field No. 11354 Pahang, 1922, named *F. lamaensis* by C. G. Lloyd. Clemens 4552, Philippine Fungi, Luzon, 1924, named *F. lamaensis* by C. J. Humphrey.

The fruit-bodies are effuso-reflexed. They are superficially indistinguishable from small specimens of *F. lamaensis* and from typical specimens of *F. noxius*. The skeletals of the flesh are about the same size as those of *F. noxius* but there are abundant hymenial setae in the tubes, just like those of *F. lamaensis*. It is thus intermediate in these characters and, as one might expect from the width of the hyphae, the structure of the upper surface is more like that of *F. noxius*. They are perhaps the issue of a hybrid mycelium, but until this is proven and since they give the 'lamaensis-appearance' in the diagnostic section of the tubes, it is better to make them a variety of *F. lamaensis*. All the collections were saprophytic.

Fomes noxius sp. n.

F. lamaensi persimilis, sed distinguitur his modis: pilei superficie rapidius glabrescenti; margine in vivo albo, cremeo vel pallide ochraceo; tubulis brevioribus, usque 11 mm. longis; poris minusculis, 80–110μ latis; sporis majusculis, 3.5–4.5 × 3–3.5μ; *setis hymenialibus nullis; setis extrahymenialibus multo crassioribus*, in carne 4–10μ latis, in dissepimentis 9–16μ latis; hyphis generantibus 2.5–5μ latis; *mycelio saepe parasitico.*

Effuso-reflexed, pilei applanate, dimidiate, slightly ascending, up to 13.5 cm. radius, 25 cm. wide; resupinate part spreading up to 35 cm. wide.

Upperside as in *F. lamaensis, rapidly glabrescent; growing margin white, creamy white or pale ochraceous.*

Flesh 6–19 mm. thick at the base, rarely up to 5 cm. thick, 1.5–12 mm. at 5 mm. from the margin, .5–2 mm. in the resupinate part, texture and colour as in *F. lamaensis;* crust .5–1 mm. thick; black crustaceous lines and mycelial strands as in *F. lamaensis.*

Tubes short, in the first season 2–5 mm. long at the base, .3–1.5 mm. at 5 mm. from the margin, developing 2–5 layers each 1–3 mm. thick, with a thin intervening layer of flesh .5–1 mm. thick, with a total thickness up to 11 mm., carbonaceous, concolorous with *F. lamaensis;* pores as in *F. lamaensis*, rather smaller, 80–110μ wide, dissepiments 40–100μ thick.

Spores as in *F. lamaensis*, rather larger, 3.5–4.5 × 3–3.5, with one gutta 1–2.5μ wide.

Basidia and cystidia as in *F. lamaensis*, cystidia sparse.

Hymenial setae none.

Extrahymenial setae in the flesh up to 600μ long × 4–10μ wide, in the dissepiments up to 100μ long × 9–16μ wide.

Generative hyphae 2.5–5μ wide.

Hab. saprophytic or parasitic at the base of trees, in clearings, estates or secondary jungle.

Type:—Sing. Field No. 25750 on *Delonix regia*, Singapore, 1932.

EXSICCATI EXAMINED:—

Sing. Field No. 5756, Singapore, 1920, T. F. Chipp.

Sing. Field No. 8391, Singapore, 1922, named *F. lamaensis* by C. G. Lloyd.

Sing. Field No. 23168, Singapore, 1930, E. J. H. Corner.

Sing. Field No. 23741, Negri Sembilan, 1930, E. J. H. Corner.

Sing. Field No. 24486, Pahang, 1930, E. J. H. Corner.

Sing. Field No. 24851, Pahang, 1931, E. J. H. Corner.

C. F. Baker No. 5423, Singapore, 1917, named *Polyporus Williamsii* Murr. by N. Patouillard.

Elmer No. 7556, Luzon, P.I., 1903, named *Pyropolyporus Williamsii* ? by W. A. Murrill.

Peradeniya Herb. No. 5412, named *F. lamaoensis* by C. G. Lloyd.

That this species is the cause of the Brown-root of rubber trees, I have proved by examining specimens of the fungus from diseased trees in Malaya, as well as one of the collections from Ceylon which Petch sent to Lloyd for determination. I presume that it causes the Brown-root of tea-bushes too, though I have not had the opportunity of examining specimens. It is also the suspected cause of the stem-rot of the oil-palm (*Elaeis guineensis*) in the East Indies. I examined several specimens from diseased palms, which Thompson submitted for identification, and it is the species referred to in his paper as 'Fomes sp. resembling *F. pachyphloeus* Pat.': (I was first struck by the large size of the extrahymenial setae in the dissepiments, which are like those of *F. pachyphloeus* rather than *F. lamaensis*). Lately I have examined other specimens from diseased oil-palms in Sumatra and found them to be the same species. It is probably a wide-spread parasite both in Africa and the East since I have little doubt that the diseases which have been attributed recently to *F. lamaensis* will be found to have been caused by *F. noxius* (12). The only other case which I have met with is that of a Flame of the Forest tree, *Delonix regia*, in the Singapore Botanic Gardens; the fungus, which had evidently entered by the roots, developed fruit-bodies at the collar of the tree and caused the branches to die-back to such an extent that the tree had to be cut down. I have not found it parasitic in the forest.

I made several observations on the rate of development of the fruit-bodies as they came up on some logs in the Botanic Gardens: I had the logs put in a shady place and well watered except in rainy weather.

The primordium appears on the surface of the wood as a minute, creamy white, villose speck, .5–1 mm. wide. It does not develop straightaway into the hemispherical primordium of the pileus even on vertical surfaces but it grows at the periphery over the surface of the wood to form a circular, or irregular, resupinate patch about .5 mm. thick. The rate of marginal growth of this patch, *i.e.* the

rate of increase in radius, varies considerably according to the supply of water, the humidity of the air and the age of the patch. The maximum rate which I obtained was 2 mm. *per diem* (24 hours). If conditions are favourable, it appears that a rate of 1–1.5 mm. *per diem* is soon reached and may be maintained until the patch is 10 cm. wide and possibly more. But if the air is dry, growth is much impeded and the rate falls to .1–.3 mm. *per diem*; in several cases, even though the logs were watered heavily twice daily, growth ceased altogether in sunny rainless weather.

When the resupinate patches are 10–16 mm. wide, pores develop over the centre and a pore-field travels centrifugally at a distance of 2–3 mm. from the margin. On vertical surfaces pilei do not develop until the patches are 2–4 cm. wide and in some cases not until they are 12 cm. wide. If the resupinate patches developed on the underside of the log, then no pilei were formed, of course, until the margin of the resupinate part had spread on to an ascending surface.

The pileus arises as a short horizontal ridge, 2–12 mm. long, from some part of the resupinate patch through the proliferation of the hyphae of the dissepiments, occasionally at the margin. The rate of marginal growth, *i.e.* the increase in the radius from the centre of attachment to the free margin of the bracket, corresponds with that of the resupinate part. The maximum rate which I observed was 1.6 mm. *per diem*. The growing margin of the pileus is as susceptible to dry air as that of the resupinate part, being very easily checked by a rainless day or two, though similarly under favourable conditions it appears that a rate of 1–1.5 mm. *per diem* is soon attained. I did not succeed in growing pilei larger than 3.5 cm. in radius and 6.8 cm. wide, but one of these had a rate of marginal growth of 1.6 mm. *per diem* when 3.2 cm. in radius. Doubtless in large specimens the rate declines even under the most favourable conditions, as in *F. levigatus*.

When marginal growth is arrested for several days, the surface of the fruit-body blackens owing to the agglutination of the hyphal ends, and the fruit-bodies may remain in this state for any length of time up to 3 months, at least, and still be able to revive on the return of wet weather. In reviving, lateral hyphae sprout from the margin and underside, sometimes from the upperside also, and cover the fruit-body with a fresh, creamy white down: then the radial growth of the limb and the downgrowth of the tubes continue. These successive additions can easily be recognised in the structure of the fruit-bodies since a thin crustaceous line extends through the flesh from the upper surface to the tubes where marginal growth has been arrested, and there are often thin layers of flesh between the successive layers of tubes.

These observations on the rate of growth are confirmed by Thompson's on the development of the fruit-bodies on the trunks of oil-palms. A bracket, 5 cm. in radius, took two months to develop, that is to say, at an average rate of marginal growth of .8 mm. *per diem.* On account of the slow growth and the extreme susceptibility to dryness, the fruit-bodies which develop under estate-conditions, like those of *Ganoderma pseudoferreum* (1), are usually stunted and small, often abortive and mostly resupinate, and have several short layers of tubes. The resupinate state might easily be mistaken for a Poria, as Patouillard mistook a similar state of *F. lamaensis,* and the species may have been described previously as a Poria. And as Petch has shown, the superficial sterile mycelium, which has projecting extrahymenial setae, was put originally in Hymenochaete with the *nomen nudum, H. noxia* Berk.

Fomes pachyphloeus Pat.

Sessile, bracket-shaped, horizontal, usually thick, applanate, often becoming subungulate, sometimes with a small resupinate foot, rarely in small specimens effuso-reflexed; up to 24 cm. in radius, 45 cm. wide, with the vertical margin up to 10 cm. high.

Upperside distantly sulcate, occasionally rugulose or coarsely tuberculate, finely velutinate or matt, *light fulvous* or dull brown, *becoming glabrous and dull black* from the centre outwards, *often cracking irregularly into small areas on drying; margin very thick,* obtuse, finally often stepped, *light fulvous.*

Flesh usually *thick,* 1.2–13 cm. at the base, 2–14 mm. at 5 mm. from the margin, *sappy-woody drying light and fibrous, fulvous or light cinnammon-fawn,* with white mycelial strands radiating from the base and a hard carbonaceous black crust, 1–2.5 mm. thick, at the surface; without carbonaceous lines in the tissue or very occasionally with one or two thin lines at the base.

Tubes *long,* in the first season 12–24 mm. long at the base, .5–3.5 mm. at 5 mm. from the margin, developing indistinct layers each 3–20 mm. thick in perennial specimens and reaching a total thickness of 17.5 cm., without intervening layers of flesh or with very thin layers less than .5 mm. thick, slightly darker brown than the flesh, of similar texture; *pores* minute, round, 55–100μ wide, dissepiments 40–110μ thick, *pale cinnammon-fawn* drying darker.

Spores as in *F. lamaensis,* 4–6 × 3.5–4.5μ with one gutta, .5–2μ wide; the old spores in the tubes with pale yellow walls.

Basidia subclavate, 9–11 × 4–6μ with 4 sterigmata 2–2.5μ long.

Cystidia as in *F. lamaensis,* sparse, 12–25 × 2–4μ.

Hymenial setae abundant, often in small groups, conical and more or less ventricose, very variable in shape, often curved or arcuate, with thick dark brown walls, narrow lumen and pale acute straight or hooked apex, sometimes 2–3-fid at the base, 13–35 × 4–10μ.

Extrahymenial setae up to 600μ long × 8–17μ wide in the flesh, 40–300 × 9–17μ in the dissepiments.

Generative hyphae 1.5–5μ wide.

Hab. saprophytic or parasitic on tree-trunks in forest.

EXSICCATI EXAMINED:—

Sing. Field No. 5563, Selangor, 1920.
Sing. Field No. 23169, Perlis, 1929.

Sing. Field No. 23698, Selangor, 1930.
Sing. Field No. 23710, Negri Sembilan, 1930.
Sing. Field No. 24197, Pahang, 1930.
Sing. Field No. 24491, Johore, 1931.
Bur. Sci. Man. No. 4551, P.I.
Bur. Sci. Man. No. 50128, P.I.
Bur. Sci. Man. No. 50129, P.I.
Bur. Sci. Man. No. 50130, P.I.

This species is common and widely distributed in Malaysia. It appears to be common also in Africa (10) and it has been reported from the West Indies (11). As a parasite, in Malaya, it seems to prefer leguminous trees. I have found it on several occasions on species of Dialium, which are large timber-trees of the top storey in the forest, and there are collections from the Angsana (*Pterocarpus indicus*) and the Rain-tree (*Pithecolobium saman*) in the Singapore Herbarium. It has not been reported from estates. Saprophytically, it seems, like many other lignicolous fungi, to prefer fig-trunks, doubtless because the wood is soft and easily decayed. In the mountains its place seems to be taken by *F. melanodermus* Pat., which is a distinct species though of similar construction, as I shall show in a subsequent paper.

The largest single pileus ever reported among the Polyporaceae belongs to this species. Lloyd found a specimen from Java in the herbarium at Leiden which was a subungulate bracket 150 cm. wide (probably 80 cm. in radius), though the details are not certain for on an earlier page he remarks that it was 250 cm. wide (4)! In Malaya fruit-bodies 12–20 cm. in radius and 20–30 cm. wide are frequent but I have not found them larger than recorded in the description. Those of *F. setulosus* and *Ganoderma fusco-pallens* (Bres.) Humphr. are often larger and much denser.

Macroscopically the fruit-bodies are almost as variable as those of *F. lamaensis*. The thickness of the flesh differs greatly and depends primarily on the size reached by the primordium before the margin of the pileus develops. A specimen in Peradeniya Herb. No. 4946 is a hemispherical primordium, 13 cm. wide × 9.7 cm. in radius, without a trace of tubes or crust. In other cases the primordium may be only 6–10 mm. in radius when marginal growth of the pileus begins. The upper surface may be extensively velutinate or rapidly glabrescent; it is never as velvety as in *F. lamaensis* because the crust always develops close to the surface. The upper surface may also be hispid, especially near the margin, owing to the projecting extrahymenial setae, and I have made a new variety on the extreme development of this character. Some fruit-bodies, too, are persistently applanate and others become ungulate as new

layers of tubes are added. The shapes which the large fruit-bodies assume when they have been growing seasonally depend chiefly on the direction of marginal growth and on the part of the marginal zone where the hyphae break out at the beginning of each season: the point must be developed subsequently.

Microscopically fruit-bodies differ in the abundance of the hymenial setae for they may occur thickly in clusters in some and be so rare in others that they can easily be overlooked: when the setae are abundant the transitions to the extrahymenial setae are also abundant, Text-Fig. 8. In some collections also most of the hyphae are 3–5μ wide; in others they are mostly narrow, 1.5–3.5μ wide. It is unprofitable, however, to make varieties in most cases even though the variations are hereditary, because they can be combined in so many different ways.

In all the descriptions of this species, published hitherto, the spores are given as pale yellow. The case is the same as that of *F. senex* (3). The old spores caught up in the tubes have pale yellow walls but the fresh spore-print is white: the fresh spores, like those of *F. lamaensis* and *F. noxius*, have colourless, hyaline walls. In the same way the subhymenial hyphae are colourless when living, but as they collapse and become agglutinated their walls also become pale yellow.

There are no records on the rate of growth, but some inferences can be drawn from specimens which I found round Tembeling in Pahang in November, 1930. In December, 1926, at the end of the rainy season, a great many trees in the riverside forest were killed by the disastrous flood of the Pahang River and its tributaries. On visiting the damaged areas some 4 years after, numerous fruit-bodies of *F. pachyphloeus* were found on the fallen trunks. The largest were 18 cm. in radius and 34 cm. wide, with the tubes 4.5 cm. long. They could not have been more than 3½ years old, allowing, that is, a few months for vegetation before the primordia emerged. Growth is therefore rapid as one would expect from the light texture and the scarcity of thick-walled hyphae.

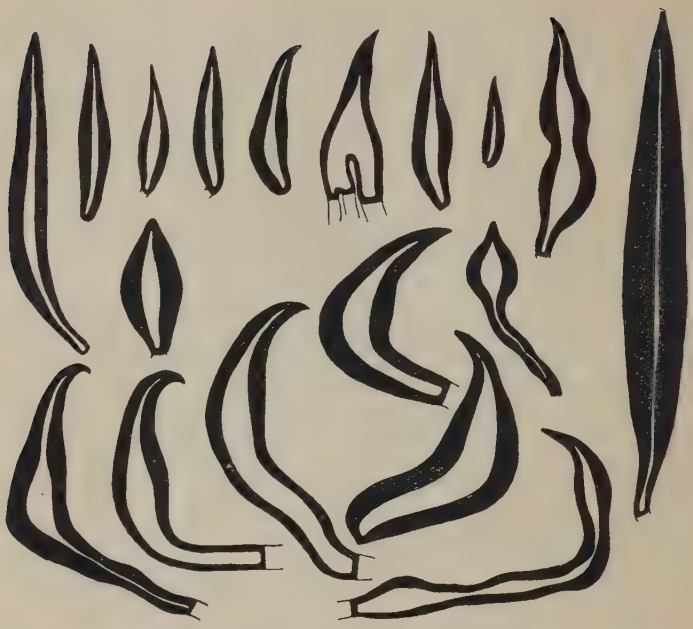
As mentioned previously, the detached fruit-bodies are unable to survive desiccation.

F. pachyphloeus var. **hispidus** var. nov.

A forma typica differt setis extrahymenialibus e superficie pilei usque 350μ excrescentibus, ergo pilei superficie minute et dense hispida.

Type:—Sing. Field No. 24500, Negri Sembilan (Jelebu), 1930.

The hymenial setae are very sparse and the generative hyphae narrow, 1.5–3.5μ wide. The fruit-bodies were saprophytic.



Text-Fig. 8. Hymenial setae of *F. pachyphloeus* in the upper row, and transitions to the extrahymenial setae of the dissepiments below and on the extreme right and left: the longitudinal portions of the intermediate forms are subhymenial: × 1000.

Since writing this account of the malayan material, a general history of the species has been provided by Humphrey, together with a redescription chiefly from Philippine material (13). There are no important discrepancies and the species is now established beyond doubt. Humphrey states that the extrahymenial setae do not exceed 264μ long but the measurements may have been taken only from the dissepiments; and the spores are said to vary from colourless to nearly snuff-brown, which doubtless refers to those from dried specimens which have been mounted in potash.

Humphrey has also redescribed *F. magnosporus* Lloyd. It differs from *F. pachyphloeus* chiefly in the larger spores (6.5–8.5μ, globose) and the absence of hymenial setae. In this second respect it recalls *F. noxius* but the tissue of the dissepiments is presumably not agglutinated and the extrahymenial setae are scarce.

Summary

The fungus causing the Brown-root of rubber-trees and tea-bushes is not *F. lamaensis* (Murr.). It is a distinct species which is called *F. noxius* sp. n. It is also the suspected cause of the stem-rot of Elaeis in the East.

F. noxius differs from *F. lamaensis* morphologically in the wider hyphae, in the absence of hymenial setae and in the structure of the upper surface, and biologically in being a facultative parasite and in growing in open situations, rarely, if ever, in the deep forest. *F. lamaensis* is a saprophyte in the forest and is very rarely found under estate conditions in Malaya.

The structure of the fruit-body in *F. noxius*, *F. lamaensis* and *F. pachyphloeus* is compared in detail. The fruit-bodies are characterised by being sessile and monomitic with white uniguttate spores, extrahymenial setae and a thick crust on the upperside. The differences are contrasted in detail. *F. lamaensis* and *F. noxius* are distinguished from *F. pachyphloeus* primarily by having the hyphae in the dissepiments agglutinated. A description of each species is drawn up from malayan material.

F. Williamsii (Murr.) is synonymous with *F. lamaensis*: so, probably, are *F.* (Poria) *cacao* Pat. and *F. sublamaensis* Lloyd.

Two new varieties are proposed, namely *F. lamaensis* var. *secedens* and *F. pachyphloeus* var. *hispidus*.

The mycological meaning of the variable characters 'velvetiness of the upper surface' and 'colour of the flesh' in *F. lamaensis* is analysed in detail. It is concluded that they have no systematic worth in the present state of knowledge.

Under favourable conditions the bracket-shaped fruit-bodies of *F. noxius* grow in radius at a rate of 1–1.6 mm. per 24 hours: marginal growth is greatly retarded or inhibited when the relative humidity is much below saturation. The fruit-bodies are degenerate and are preceded even on vertical surfaces by a resupinate 'Poria-stage' of varying extent.

The fruit-bodies of *F. pachyphloeus* evidently grow much more rapidly. On vertical surfaces those of *F. pachyphloeus* and *F. lamaensis* are preceded by a typical primordial knob without a 'Poria-stage.'

In none of the three can detached fruit-bodies survive desiccation, even if only for a few days.

Though a facultative parasite, *F. pachyphloeus* has not been found to cause any disease in estates in Malaya.

In conclusion I must offer my sincere thanks to those who so willingly lent herbarium-material at my request, and without whose co-operation this problem could not have

been solved: to the Director of the New York Botanic Gardens for the types of *F. lamaensis* and *F. Williamsii*: to the Director of the Royal Botanic Gardens, Peradeniya: to the Director of the Experimental Station of the A.V.R.O.S., Medan, Sumatra: to Dr. C. J. Humphrey for material from the Philippine Islands: and most especially to Mr. A. Thompson who first brought the problem to my notice, and to Miss E. M. Wakefield and Mr. A. Sharples for their expert assistance in matters systematic and pathological.

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